Variation in *Cronartium ribicola* Field Resistance Among 13 *Pinus monticola* and 12 *P. lambertiana* Families: Early Results from Happy Camp

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Abstract—In 1995 seed from 13 *Pinus monticola* (western white pine) and 12 *P. lambertiana* (sugar pine) parents previously included in short-term blister rust testing at Dorena Genetic Resource Center (DGRC), Cottage Grove, OR, were sown to establish field trials. The parents were chosen to represent a wide array of resistance responses shown in earlier artificial inoculation trials. Percentage stem symptoms (cankers and bark reactions) in 1999 and 2000 at the 1996 Happy Camp (HC) trial are reported here. Sugar pine families have a higher percentage of trees with stem symptoms (SS percent) than do western white pine families. In addition to a greater susceptibility to infection overall, the major gene resistance present in several of these sugar pine families (conferred by Cr1) is ineffective due to the relatively high frequency of a virulent (vcr1) strain of rust at this site. Western white pine families varied from 10.4 to 83.3 SS percent and sugar pine from 73.5 to 91.8 SS percent. The susceptible control lot for western white pine showed a much greater percentage of trees with stem symptoms (83.3 percent) than any other western white pine seedlot. The two western white pine families with known major gene resistance (Cr2) were among the families with lowest infection at this site. The resistance mechanism of the family with the second lowest level of stem symptoms is unknown. Moderately strong and significant positive correlations ($r>0.69$, $p<0.05$) existed between SS percent at HC and SS percent following artificial inoculation at DGRC. The correlation between needle lesion frequency in DGRC screening and stem symptoms observed at HC was positive but non-significant ($r>0.5$, $p>0.1$ for sugar pine and western white pine).

Key words: *Pinus monticola*, *Pinus lambertiana*, blister rust, Cr1.

Introduction

In Oregon and Washington, the USDA Forest Service (Region 6) began selecting and screening parent trees of western white pine (*Pinus monticola* Dougl. ex D. Don.) and sugar pine (*P. lambertiana* Dougl.) for resistance to white pine blister rust (*Cronartium ribicola* J.C. Fisch) in the late 1950s. Over 9500 parent trees of these two species have been selected for rust resistance in natural stands, but variation in rust hazard by site influences the expected efficacy of field selection. Progeny of these field selections have been screened for resistance at Dorena Genetic Resource Center (DGRC) (Sniezko 1996, Kegley and Sniezko this proceedings). Selections from rust screening have been used to establish seed orchards in many of the breeding zones, and resistant seed is now available for some zones.

Operational screening at DGRC generally involves a single inoculation using two-year old seedlings and the subsequent assessment of seedlings and assignment into resistance categories. Primary categories of response in seedlings are lack of visible stem infections versus presence of visible stem symptoms. Seedlings screened at DGRC are assigned to these two categories and are also assessed for other resistance responses (Sniezko 1996, Kegley and Sniezko this proceedings). Some of the mechanisms preventing stem infection include: hyper-sensitive reactions (HR) in the needles conditioned by major genes in sugar pine (Cr1) and western white pine (Cr2) (Kinloch and Comstock 1981, Kinloch and others 1999, Kinloch and Dupper 2002), and two mechanisms hypothesized to be controlled by single recessive genes: (a) fungicidal reaction in the short shoot (Hoff and McDonald 1971, McDonald and Hoff 1971), and (b) premature shed of secondary needles (McDonald and Hoff 1970, McDonald and Hoff 1971). Resistance mechanisms that may reduce the number of stem infections or the severity of these infections include: (a) bark reaction (Hoff 1986, Kinloch and Davis 1996), (b) reduced needle lesion frequency (Hoff and McDonald 1980a, Meagher and Hunt 1996) and (c) tolerance (Hoff and McDonald 1980b). These mechanisms have been at the core of the Region 6 selection program for three decades; however, for both sugar pine and western white pine there has been little or no formal field validation of the test results from the artificial inoculation and screening at DGRC or tracking of individual family rust resistance over time.

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Field trials were established in 1996 and 1997 with seedlings from 13 western white pine and 12 sugar pine families in the first of a series of validation plantings. These 25 seedling families were planted at three test sites, two in Oregon and one in California. The first and largest was planted at Happy Camp, California in 1996. This site was also the first one to show moderate levels of rust infection. The Happy Camp site on the Klamath National Forest has been the principal field test site for blister rust resistance evaluation for the Forest Service's Region 5 (California) sugar pine program since 1962 (Kinloch and Byler 1981). This test site has a high frequency of a strain of blister rust virulent to the major gene resistance conferred by the Cr1 gene in sugar pine (Kinloch and Comstock 1981). Since Cr1 is neutralized on sugar pine at this site, it is possible to observe resistance(s) that would be masked by Cr1 at other sites. The main purpose of these field trials is to validate the effectiveness and durability of the putative mechanisms of resistance to blister rust.

This paper examines results five years after planting and assesses species and family differences in percentage of trees with stem symptoms (SS percent). We also report on the correlations between field results (for SS percent) and results from operational screening of seedlings at DGRC (SS percent and needle lesion frequency).

Materials and Methods

Twenty-five seedlots (13 western white pine and 12 sugar pine) were selected from relatively recent blister rust screening trials ("runs") at Dorena Genetic Resource Center (DGRC). Two of the western white pine seedlots are full-sib families from crosses made among resistant parents in DGRC orchards, and one of the western white pine seedlots is a wind-pollinated collection from a seed orchard at DGRC. The remaining 22 families are open-pollinated from select trees in natural stands. The families selected for these field tests cover a wide range of geographic areas in Oregon and Washington as well as an array of resistance responses observed in five years of assessments following artificial inoculation at DGRC. Families that displayed little or no resistance in a previous DGRC test were included as low resistance controls.

Seed was sown in containers in spring 1995, and seedlings were planted at Happy Camp (HC) in a randomized complete block design in spring 1996 after budbreak. Twelve blocks were established with generally four trees per family per block although a few families had fewer trees per block, and an occasional container held two seedlings that were then planted together. *Ribes sanguineum* Pursh, an alternate host to *C. ribicola*, was inter-planted among the pines to help ensure uniform exposure to the rust.

Height as well as number and type of stem symptoms (SS) were assessed in June 1999 and July 2000 at Happy Camp. For the main analysis in this paper, a tree was recorded as having SS if there was any sign or symptom of rust infection on the bole or branches, including small orange discoloration at the base of infected needles (the initial signs of stem infection), normal cankers or bark reactions in either 1999 or 2000. Percentage of trees with stem symptoms (SS percent) was tabulated by family plot and used for analyses. Analyses of variance were performed using SAS Proc GLM (SAS Institute 1999) to assess differences between species and families within species for SS percent.

Pearson's correlations between family mean SS percent at Happy Camp and family mean SS percent and Needle Lesion class (NLclass) at DGRC were calculated using SAS Proc CORR (SAS Institute 1999). The correlations use results from the 1995 sowing for the 19 families tested in that year, and a second set of correlations uses the 1995 test data plus results for the six families tested in other screening trials (table 1). NLclass is a family and trial-specific value based upon number of needle lesions or "spots" on all secondary needles on each seedling (Table 2). NLclass values range from 0 to 4. Generally, the scale is set up to have approximately 25 percent of the seedlings in each needle lesion class from 1 to 4; seedlings in needle lesion class 0 have no spots.

Results

Sugar pine had a higher percentage of trees with stem symptoms (SS percent) than western white pine at the HC site (fig. 1). Highly significant differences ($p<0.0001$) for SS percent existed between species and among western white pine families ($p<0.0001$) but not among sugar pine families ($p=0.58$). Except for the susceptible western white pine (control) family, there was no overlap in SS percent among the 12 sugar pine families and the 13 western white pine families (fig. 1). Most of the stem symptoms are from infection in autumn 1997.

Overall SS percent (SS observed in 1999 and/or 2000) was 85.4 percent for sugar pine and 43.2 percent for western white pine (fig. 2). Mean SS percent for western white pine was 35.2 percent in the 1999 and 30.1 percent in the 2000 (fig. 2). Ten of the 13 western white pine families had lower SS percent in 2000 than in 1999. SS percent in sugar pine increased from 70.8 percent in 1999 to 77.4 percent in 2000 (fig. 2). Only one sugar pine family had a lower SS percent in 2000 than in 1999, and two families had the same SS percent in 1999 and 2000. There was a relatively narrow range in SS percent among sugar pine families (73.5 to 91.8 percent) but a very wide range among western white pine families (10.4 to 83.3 percent).

Of two western white pine families notable for their very low SS percent (table 1 and Fig. 1), Family #22 is known to have major gene resistance (from Cr2); the resistance mechanism for the other family (#18) is unknown, but it is not Cr2. The low resistance western white pine control (#16) had the highest SS percent (table 1).

Strong and significant correlations exist between family mean SS percent at Happy Camp and those from 1995 artificial screening at DGRC for both sugar pine ($r = 0.73$, $n=9$, $p=0.024$) and western white pine ($r = 0.70$, $n=10$, $p=0.026$) (also see fig. 3a and 3b). There were positive but non-significant correlations between needle lesion frequency (NLclass) in DGRC screening and SS percent at Happy Camp for both species (fig. 4a and 4b). Even western white pine family #25, which was outstanding for NLclass in several tests at DGRC, is only average for SS percent at HC (table 1).

Table 1—Summary results for percent stem symptoms, needle lesion class, and major gene resistance from Dorena rust-screening and Happy Camp, California field planting for 12 sugar pine (SP) and 13 western white pine (WWP) families.

Field ID	Female parent	Male parent	Species	MGR assessment results[b]	Test year[c]	Needle lesion class[d]	% Stem symptoms	
							Dorena	Happy Camp[f]
1[a]	02176-040	wind	SP	—	1992	3.25	100.00	89.58
2	10045-689	wind	SP	—	1995	2.53	100.00	91.83
3	11052-570	wind	SP	not yet tested	1992	1.75	48.33	87.76
4	11054-370	wind	SP	—	1992	1.93	100.00	80.56
5	11054-419	wind	SP	Cr1 (~52%)	1995	1.64	32.20	81.63
6	11054-581	wind	SP	non-Cr1	1995	2.49	100.00	82.22
7	11054-776	wind	SP	—	1995	3.30	85.19	88.89
8	11054-903	wind	SP	Cr1 (~21%)	1995	2.00	43.10	73.47
9	18032-608	wind	SP	—	1995	1.46	92.59	85.71
10	18033-431	wind	SP	—	1995	2.30	96.30	87.50
11	18034-404	wind	SP	—	1995	3.02	94.92	87.50
12	20045-001	wind	SP	non-Cr1	1995	3.54	96.61	89.80
13	11053-552	wind	WWP	—	1995	1.48	88.33	38.10
14	03023-509	wind	WWP	—	1995	2.32	100.00	50.00
15	03024-510	wind	WWP	non-Cr2	1995	1.75	70.00	32.65
16[a]	03024-532	wind	WWP	non-Cr2	1995	3.33	98.33	83.33
17	03024-793	wind	WWP	—	1995	2.43	91.38	53.19
18	05081-003	wind	WWP	non-Cr2	1995	1.92	40.00	12.25
19	06023-521	wind	WWP	not yet tested	1995	1.73	74.51	60.00
20	18034-140	wind	WWP	non-Cr2	1995	2.82	96.67	40.39
21	1803.5-150	wind	WWP	non-Cr2	1995	1.95	90.00	57.45
22	15045-816 x 15045-841	wind	WWP	Cr2 (97%)	1989	2.53	17.02[e]	10.42
23	15045-823	15045-840	WWP	Cr2 (~75%)	1988	2.62	42.50[e]	33.33
24	21105-052	wind	WWP	non-Cr2	1995	2.78	89.83	44.44
25	18033-708	18033-703	WWP	non-Cr2	1988	0.43	23.33	45.83

[a]Susceptible control family based on performance in a single artificial inoculation trial at DGRC

[b]Results from separate inoculation to score hypersensitive reaction (HR) on needles and classify families as to presence or absence of major gene resistance. Percentage seedlings exhibiting HR indicated in parentheses. Preliminary information indicates the female parent of Family 22 (Orchard Accession # 023220) may be homozygous dominant for HR.

[c]Test year refers to the year in which the family was sown at Dorena; inoculation occurred the following year.

[d]Family mean needle lesion class at DGRC based on the number of lesions on all secondary needles approximately 9 months after artificial inoculation with *C. ribicola*.

[e]In many years the mixture of spores used for inoculation at DGRC contained an unknown frequency of a strain of rust virulent to Cr2 in western white pine.

[f]Overall percent stem symptoms (present in 1999 and/or 2000) at Happy Camp.

Table 2—Number of needle lesions in each class by test year and trial at Dorena Genetic Resource Center.

Test year	Trial	Species	Needle lesion class[a]				
			0	1	2	3	4
1988	4	western white pine	0	1	2-3	4-6	7+
1989	4	western white pine	0	1-3	4-9	10-19	20+
1992	4	sugar pine	0	1-10	11-26	27-50	51+
1995	1	western white pine	0	1-3	4-9	10-20	21+
1995	2	sugar pine	0	1-3	4-9	10-27	28+

[a]Each seedling is evaluated for number of needle lesions ("spots") present on secondary needles and is assigned to a "needle lesion class." Needle lesion classes are based on counts of number of spots on seedlings in monitoring plots and are trial specific. Family mean needle lesion class is the average of all living seedlings in a family.

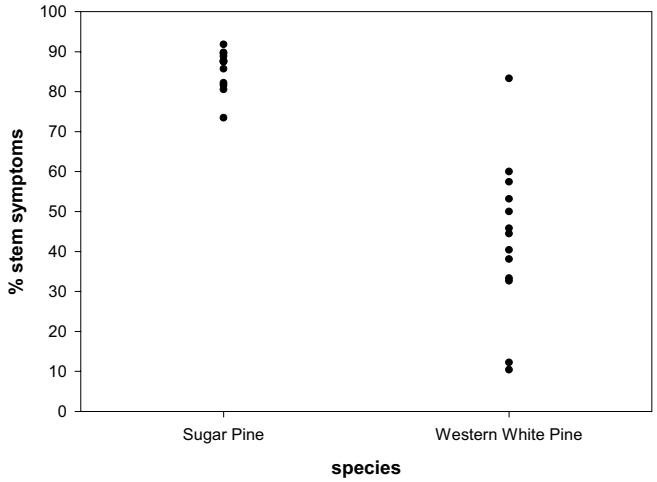

Figure 1—Range of means for overall percent stem symptoms at Happy Camp for 12 sugar pine and 13 western white pine families.

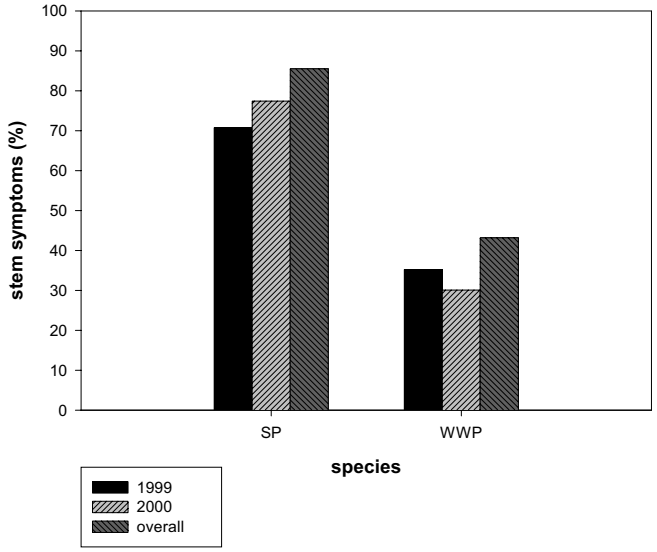

Figure 2—Species means for 1999, 2000, and overall (present in 1999 or 2000) percent stem symptoms for 12 sugar pine and 13 western white pine families outplanted at Happy Camp, California.

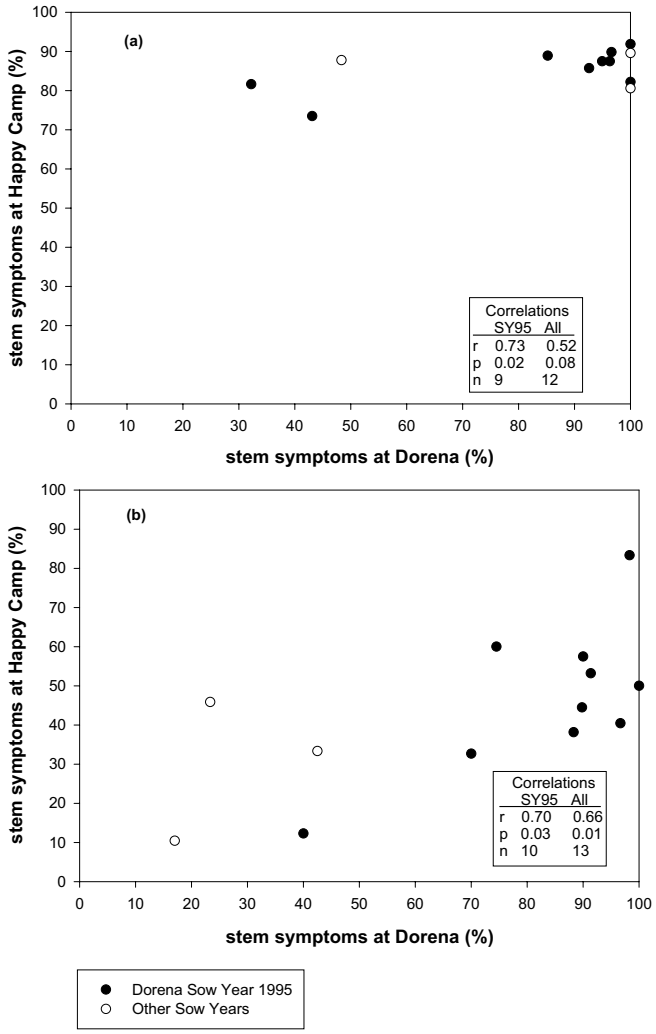

Figure 3—Percent stem symptoms at Happy Camp vs. percent stem symptoms at Dorena for (a) 12 sugar pine families and (b) 13 western white pine families.

Discussion and Summary

The results clearly show that after five years at HC, sugar pine is significantly more susceptible to blister rust than western white pine. In a summary of previous studies involving 16 species of five-needle pines, western white pine appeared to be slightly less susceptible than sugar pine (Bingham 1972). In 1999 at HC, sugar pine had 2.7 times as many stem infections as western white pine (953 vs. 356 total stem infections, Sniezko and others 2000).

Current results from HC demonstrate that SS percent at this site corresponds fairly well to SS percent at DGRC. However, at the current level of infection, there appears to be little or no differentiation between families showing different levels of needle lesion frequency at DGRC and SS percent in the field for either western white pine or sugar pine. Needle lesion frequency may be more associated with number of stem infections rather than presence or absence of stem infections. It is still too early to discern the relationships of other resistance traits at DGRC and in the field.

In examining SS percent by individual year, it was noted that from the 1999 to the 2000 assessment there was a slight increase (6.7 percent) for sugar pine but a decrease (5.2 percent) for western white pine, and that the total for either year was more than 8 percent lower than the overall SS percent (SS present in 1999 or 2000) (fig. 2). Close re-examination of a few trees in spring 2001 showed some small, fading stem symptoms that could have easily been missed and will probably not be visible at all within a year or two.

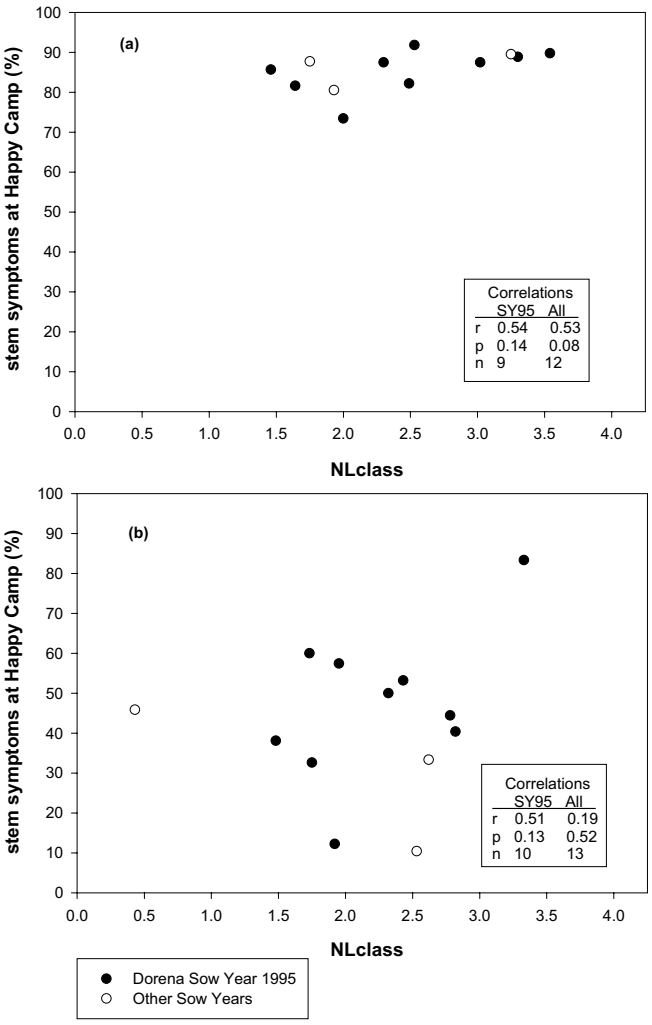

Figure 4—Percent stem symptoms at Happy Camp vs. needle lesion class (NLclass) at Dorena for (a) 12 sugar pine families and (b) 13 western white pine families (see table 2 in text for needle lesion classes).

Although the percentage of sugar pine infected at HC is already high, there is little mortality as of July 2000. On this site the sugar pine families with HR show high levels of infection because of the high frequency of the vcr1 gene (virulent to Cr1) in the rust population at HC; these two families would be expected to show much lower infection at most sites. The lack of significant differences in SS percent among families in sugar pine may not be a true measure of field resistance; future assessments will determine whether differences in bark reaction, mortality or tolerance exist among families.

One of the biggest expected changes over the next ten years would be the performance of the two western white pine families with Cr2 (Families 22 and 23) if a strain of rust with specific virulence to Cr2 (vcr2) became prominent at this site. The virulent strain is known to be present in a small adjacent test established in 1971 (Kinloch, personal communication). Previously, vcr2 had only been documented in a localized area in Oregon (Kinloch and others 1999, McDonald and others 1984), but a recent survey has demonstrated its presence in varying frequency in parts of western Oregon and at Happy Camp, CA (Sniezko and others 2001).

The performance of the Cr2 families in this test demonstrates that there may be important geographic differences in blister rust resistance. The resistance conferred by the Cr2 gene in western white pine appears to be limited geographically to California, Oregon, and southern Washington (Kinloch and others 2003), but there may also be other types of resistances that are geographically restricted and not noted in earlier findings (see discussion below). Elucidation of geographically restricted resistance mechanisms would aid breeding efforts and establishing deployment strategies for resistant seed. At present, operational rust screening at DGRC and elsewhere only discerns categories of phenotypic expression, but it is possible that several mechanisms may have only minor differences in their gross physical expression. For example, only in the mid-1990s has DGRC incorporated an operational screening procedure that separates a major gene for resistance (hypersensitive reaction in the needles, see Kinloch and others 1999, Kinloch and Dupper 2002 for details) from other resistance mechanisms in western white pine that also lead to canker-free seedlings after inoculation such as needle shed or short shoot (Hoff and McDonald 1971, McDonald and Hoff 1970, Sniezko and Kegley 2003).

The low level SS percent in Family #18, an open-pollinated, non-Cr2 western white pine family, might be due to some combination of needle shed or short shoot mechanisms (both purportedly due to single recessive genes). If this were true, the frequency of these genes in natural stands would have to be high and there is no evidence of this in testing at DGRC; the great majority of families show greater than 90 percent infection in screening trials at DGRC. This could also be a previously undefined mechanism (mechanism 'X'), characterized by low incidence of stem symptoms at DGRC in testing (35-60 percent SS, relative to 90-100 percent for most other open-pollinated families) and a negative result for presence of Cr2 resistance in a separate test. Family #18 at HC fits these parameters. The relatively low SS percent for this open-pollinated family at DGRC suggests the involvement of a single major gene, but the very low SS percent at HC suggests a more complicated scenario. Some differences in performance of families in short-term screening and in the field are not unusual. In a summary of studies in other plant species Keller and others (2000) note that the resistance phenotype may vary between tests performed under controlled conditions versus field conditions, or between seedlings and adult plants. From operational screening of thousands of western white pine parents at DGRC it appears that a very low frequency of parents with this type of resistance (low SS percent and non-Cr2) is present in much of Oregon and Washington (unpublished data).

Artificial inoculations and short term screening at DGRC provides a potentially more time- and cost-efficient method of evaluating progeny of thousands of parent trees for an array of resistance mechanisms than costly, long-term field trials. However, field tests are essential for validating effectiveness of the various resistance responses characterized on young seedlings following artificial inoculation. A wide array of rust races can be included in artificial screening,

whereas field testing at any one site would generally rely on local populations of the pathogen, which may vary from year to year. However, due to the limitations of a single inoculation on very young seedlings, resistance mechanisms that manifest themselves more clearly on older, larger trees in the field may not be identified in operational screening (such as ontogenetic resistance (Kinloch and Davis 1996); low canker frequency (Sniezko and others this proceedings)), thus field plantings serve a complementary function. Correspondence between results from short-term testing at DGRC and long-term field testing may be dependent upon factors influenced by the environment, the rust population, and the nature of the families and resistance mechanisms under test.

Results from these field tests will allow confirmation of the field effectiveness of resistance responses observed on seedlings following artificial inoculation, as well as provide demonstrations to land managers hoping to use western white pine or sugar pine in restoration or reforestation plantings. The plantings will also serve as monitors to changes in virulence of the rust, and they may help detect resistance mechanisms or other events not apparent in short-term screening. For example, from recent observations in fall 2001, some cankers appear inactive but do not fit the classic pattern of bark reactions.

It may also be very useful to establish some joint field tests among the blister rust programs in Oregon, Washington, Canada, Idaho, and California using a small number of families selected for specific resistance responses in these different locations. Such plantings may help discern the presence of geographically limited mechanisms or the influence of environment and local rust populations on host resistance.

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